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BREEDING PLANTS OF THE CABBAGE GROUP

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INTRODUCTION

A large number of the world's vegetable crops belong to the genus *Brassica* of the family Cruciferae. These cultivated forms are old; they apparently originated in Europe, particularly in the region bordering the North and Baltic seas, and on the Italian peninsula. From the south came broccoli, and from the north our domestic cabbage, Brussels sprouts, and kale. All these diverse forms are thought to have sprung from one wild type now found on the cliffs of the coastal regions of western Europe. Although forms of *Brassica oleracea* L. have been cultivated for over 4,000 years (Hayes and Garber)[(5)], the improvement of the varieties has, apparently, taken place mostly within the last 400 years.

While the forms of *Brassica oleracea* are exceedingly diverse, this one species being divided into botanical varieties, these into horticultural varieties, and the latter again into strains, a casual survey of even the most carefully produced strain of any one variety will show it to be very variable. Plant breeders have not yet been able to bring the commercial strains to the degree of uniformity reached in many other crops.

FLOWERING HABIT

Members of *Brassica oleracea* are annuals, biennials, or perennials. Sprouting broccoli is a perennial, blooming the first season; cauliflower is an annual, forming both curd and flowers the first season and dying after the seeds ripen. Cauliflower broccoli (the cauliflower which matures in early spring) is a biennial, requiring a cool dormant season for the inception of curd formation; but the plant dies when the seed has matured. Cabbage, kale, kohlrabi, and Brussels sprouts are perennials, but do not bloom until they have passed through a period of cool weather.

The wild cabbage from which the present forms have come is an annual. In cabbage the annual tendency is still present to some extent, and occasional plants are seen bolting to seed even though they have not been exposed to low temperature.

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FLORAL STRUCTURE

For intelligent breeding of any crop plant, one must understand the structure, function, and limitations of the reproductive system.

The flowers of *Brassica oleracea* are borne upon stout racemes. In cauliflower and cauliflower broccoli these racemes are often modified and shortened. A cauliflower broccoli plant will open its entire crop of 5,000 to 8,000 flowers within a period of 10 to 14 days, while the blooming season of a cabbage plant will extend over two months, or even longer if seed is not formed. The flower buds are approximately the same size and grow at about the same rate in all the different forms.

Measurements taken daily, upon several flower buds, indicate that in general 25 to 30 days must elapse between the differentiation of the meristem and the unfolding of the petals. The reduction divisions of the pollen mother cells occur in buds about 1.6 to 1.8 mm in length; those of the embryo-sac mother cell begin in buds about 5 mm long. The last division of the pollen grain occurs the day before the flower opens; the embryo sac is completely organized when the flower opens. Temperature influences to a marked degree the number of flowers that open each day, but the average is three to four to each raceme.

Anthesis, or expansion of the floral parts, usually begins about 4 to 5 P.M. The petals and stamens start to elongate and force the sepals apart. Early the next morning the petals have practically completed their growth and appear as a tightly rolled cylinder. Anthesis is completed by the reflexing of these petals to form the typical yellow cross-shaped flower.

The pollen is released early in the first day the flower is open by a longitudinal split in the anther and a reflexing movement of the anther walls. This movement is not completed for several hours.

POLLINATION AND POLLEN BIOLOGY

Insects visit the flower freely. Honeybees, although usually plentiful, often fail to be very efficient, because they do not work at temperatures below 60° F. Bumblebees are not very plentiful in California, but usually a few of them are collecting pollen in nearly every field. Representatives of several families of solitary bees visit the flowers in search of both pollen and nectar. As these bees work at lower temperatures than honeybees, they are probably a very important factor in cabbage seed production. Those collected at Davis in March included the cuckoo bee (*Nomadidae*), the leaf-cutting bee

(*Megachilidae*), and the mining bee (*Andremidae*). There were also found a few beeflies (*Bombyliidae*) in search of nectar.[3]

The pollen germinates readily in 20 per cent sucrose solution at 60° to 68° F. It germinates but weakly in 15 and 25 per cent solutions, and not at all in a 10 per cent solution.

The optimum temperature for germination is about 68° F. Germination is abnormal at temperatures of 85° or above and fails at 104°; it is slow but normal at 46°, and is negative again at 39°.

The longevity of pollen stored at different temperatures is shown in table 1. Fully opened flowers were stored in constant temperature

TABLE 1

GERMINATION OF POLLEN AFTER STORAGE AT VARIOUS TEMPERATURES*

Storage temperature, degrees Fahrenheit	First day	Second day	Third day	Fourth day	Fifth day	Sixth day	Seventh day	Eighth day	Ninth day
39	+	+	+	–	–				
52	+	+	+	+	+	+	Weak	Weak	–
68	+	+	Weak	Very weak	–	–			
86	+	+	Very weak	–					
95	+	+	–						
Greenhouse	+	+	Weak	–	–				

* The plus sign (+) indicates good germination; the minus sign (–) indicates no germination.

chambers held at the indicated temperatures. Each day some of the pollen from each anther of each flower was tested for viability. The results show that pollen was short-lived at all the temperatures used, but that relatively low temperatures prolonged its life considerably. Under ordinary field conditions pollen is not viable for longer than four days. These results in general agree with those secured by Bach(1) with rape, *Brassica napus* L.

Table 2 shows the results when pollen was taken from protected flowers of known ages in the greenhouse and applied to the stigmas of flowers not yet open. Young flowers were used to avoid difficulties arising from incompatibility as explained in a later section. These results show that pollen from flowers open as long as four days, and whose petals were withered, still gave a good set of seed.

The stigma is receptive to pollen from about five days before the flower opens until four days after (table 3). Pollen was applied to the stigmas of lower buds of various lengths. Ten hours after pollination the buds were killed in Karpechenko's solution. When sectioned and stained, pollen tubes were found in buds as small as 4.5 mm in length.

[3] These insects were identified by G. H. Vansell of the Bureau of Entomology, U. S. Department of Agriculture.

TABLE 2

Number of Seeds per Pod Obtained by Applying Pollen of Different Ages to Immature Stigmas*

Flower position	Age of pollen			
	At anthesis	After four days	After five days	After six days
1	17	9	0	0
2	16	4	0	0
3	14	15	0	0
4	19	12	0	0
5	10	6	0	0
6	12	14	0	0
7	19	12	0	0
8	16	7	3	0
9	11	13	3	0
10	17	7	4	0
11	14	8	5	0
12	10	9	3	0
13	—	4	1	—
14	—	—	2	—
Total	175	120	21	0
Average	14.58	9.23	1.5	0

* In tables 2, 3, and 6 the first column, headed "Flower position," indicates the position of the treated flower on each raceme; i.e., flower number 1 represents the lowermost flower treated and 12 represents the twelfth flower on each one. All other columns represent one raceme each.

TABLE 3

Number of Seeds per Pod Obtained by Applying Fresh Pollen to Flowers of Different Ages

Flower position	Pollen applied			
	At anthesis	After two days	After three days	After four days
1	19	0	0	12
2	17	20	0	14
3	—	20	20	0
4	13	3	15	15
5	9	15	15	13
6	13	21	16	11
7	20	20	7	13
8	15	18	9	17
9	12	21	10	11
10	13	13	15	0
11	18	13	0	12
12	20	17	15	9
13	15	20	12	10
14	14	21	20	13
15	16	15	8	12
16	13	10	18	14
17	8	20	—	0
18	12	20	—	0
19	18	21	—	—
20	14	—	—	—
Total	279	308	180	176
Average	14.68	16.21	11.25	9.78

COMPATIBILITY

Cross-pollination which is the rule in *Brassica* is usually brought about by insect visitation. Bees are the active pollinating agents. Despite study of the habits of the honeybee, comparatively little is known of the degree to which it cleans itself in the hive, and the maximum distances it will forage for food. Still less is known of the habits of the bumblebees and of the solitary bees which often outnumber honeybees in a field of blossoming *Brassica* plants.

Although the importance of insects in bringing about cross-pollination has long been known, the mechanism which insures

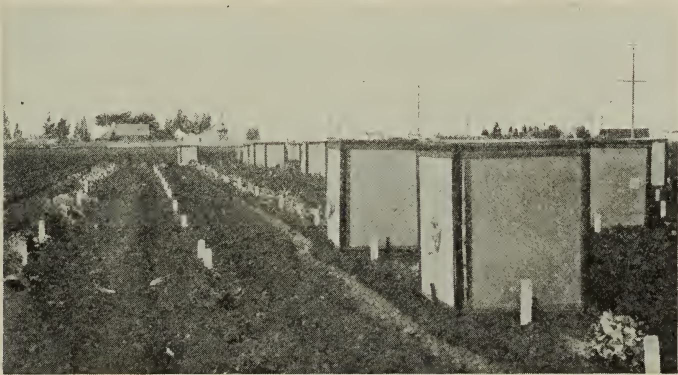

Fig. 1.—Cages for isolating entire plants singly or in groups. Ferry-Morse Trial Grounds, 1931.

cross-fertilization has only very recently been understood. Some plant breeders have attempted to isolate choice individuals under muslin cages, thus preventing cross-pollination and bringing about self-pollination either naturally or by the introduction of flies (fig. 1). Their efforts have met with but little success. Usually less than 100 seeds are formed, while similar plants cross-pollinated in the open are capable of producing a half pound each of seed. Attempts at artificial self-pollination under paper or cloth bags have met with but little more success. Nelson[7] and others observed that the seed set was nearly always in the apical end of the seed pod.

Cross Pollen More Efficient Than Own Pollen.—The greater efficiency of cross as compared with self-pollination was early recognized. Roemer[11] mixed pollen from green and red cabbage and applied it to the stigmas of emasculated flowers of the green-cabbage pollen parent. As red is dominant over green, all crossed seed would give

red plants. On germinating the seed, he secured a preponderance of red plants: 137 red and 29 green instead of the expected 84 red and 84 green.

A similar test was made at Davis, California, during May, 1930. The results of testing seven plants are shown in table 4. Own pollen was placed on each stigma on the morning when the flower opened and immediately afterward pollen from a commercial red cabbage plant was applied to the same stigma. Of the 907 seeds which germinated, only 53 were green or selfed. The approximate 6 per cent of selfed seed in this case may mean that under field conditions the proportion of about one seed in every pod results from self-pollination.

TABLE 4

RESULT OF CROSSING AND SELFING AT THE SAME TIME ON THE DAY OF ANTHESIS

Pedigree No.	Number of flowers treated	Number of seeds produced	Red seedlings	Green seedlings	Per cent green seedlings
1-4-3-107	25	292	113	7	5.8
1-4-3-101	21	201	94	3	3.1
1-6-81-117	22	430	313	26	7.7
1-6-76-107	12	64	34	2	5.6
1-6-87-2-C-9	14	157	117	8	6.4
1-4-41-2-C-8	15	245	183	7	3.7
Total	109	1,389	854	53	....
Average	....	....	....	....	5.84

The results point to some power of discriminating between own and foreign pollen when applied simultaneously. That own pollen is as effective as foreign if applied at the proper time was shown by Pearson.[10] Twenty-four cabbage plants resulting from three generations of self-pollination were tested for self fertility. In one case, own pollen was applied to the stigma of each flower after anthesis. In the other case, own pollen was applied to the immature stigmas from one to six days before the flower opened. The results, presented in table 5, show that if sufficient time be given the pollen tubes to reach the ovules, good sets of seed can be secured from self-pollination.

Cross Incompatibility.—Inbred families of cabbage are often composed of plants as incompatible to pollen of other plants of the same family as to their own pollen. Members of such a family would not produce seed if planted together and isolated from other families. That the mechanism which operates to prevent seed setting to pollen of sister plants is the same as operates to prevent seed setting to own pollen is shown by an experiment the results of which are presented

TABLE 5

SUMMARY OF RESULTS OF POLLINATING CABBAGE FLOWERS IN THE BUD AND AT ANTHESIS

Pedigree No.	Pollinated at time of anthesis					Pollinated in the bud				
	Number of flowers pollinated	Number of flowers producing seeds	Total seeds	Per cent set	Average number seeds per pod	Number of flowers pollinated	Number of flowers producing seeds	Total seeds	Per cent set	Average number seeds per pod
1-4-41-1-A	37	3	3	8	1.0	50	29	358	58	12.3
1-4-41-1-B	28	1	1	4	1.0	53	33	538	62	16.3
1-4-41-1-C	9	2	4	22	2.0	46	40	550	87	13.8
1-4-41-1-D	39	0	0	0	0.0	58	41	658	71	16.1
1-4-41-2-A	29	0	0	0	0.0	47	35	421	74	12.0
1-4-41-2-C	23	1	1	4	1.0	36	25	226	70	9.0
1-4-41-2-D	19	0	0	0	0.0	51	47	547	92	11.6
1-6-52-1-A	26	0	0	0	0.0	54	47	703	87	15.0
1-6-52-1-B	21	0	0	0	0.0	39	28	253	72	9.0
1-6-52-1-C	25	1	1	4	1.0	43	38	664	88	17.5
1-6-52-1-D	20	0	0	0	0.0	57	35	288	61	8.2
1-6-52-1-E	37	0	0	0	0.0	52	44	426	85	9.7
1-6-81-1-A	13	0	0	0	0.0	35	28	206	80	7.4
1-6-81-1-B	19	3	3	16	1.0	18	18	215	100	11.9
1-6-81-1-C	25	1	1	4	1.0	45	41	508	91	12.4
1-6-81-1-D	37	3	4	8	1.3	56	49	611	88	12.5
1-6-87-1-A	17	1	2	6	2.0	55	53	767	96	14.5
1-6-87-1-B	25	1	1	4	1.0	40	29	218	72	7.5
1-6-87-1-C	22	2	3	9	1.5	44	26	245	59	9.4
1-6-87-1-E	27	0	0	0	0.0	43	27	243	63	9.0
1-6-87-2-A	30	0	0	0	0.0	33	20	198	61	9.9
1-6-87-2-B	36	1	1	3	1.0	58	47	501	81	10.7
1-6-87-2-C	39	0	0	0	0.0	58	38	391	66	10.3
1-6-87-2-D	35	1	1	3	1.0	53	46	611	87	13.3
Total	638	21	26	—	—	1,124	864	10,346	—	—
Average				3.29	1.24				76.9	11.97

in table 6. The two plants used also appear in table 5 and were sisters in a family resulting from three generations of inbreeding. When crossed at anthesis, or after the flower had opened, no seed was produced (table 6), irrespective of the direction in which the cross was made. However, a good set of seed was produced when the pollen was applied before the flower opened. These results are very similar to those presented in table 5, the results of self-pollinating at anthesis and in the bud.

TABLE 6

RESULTS OF CROSSING TWO SISTER CABBAGE PLANTS IN THE BUD AND AFTER ANTHESIS; EXPRESSED AS NUMBER OF SEEDS

Flower position	1-4-41-1-A x 1-4-41-1-C		1-4-41-1-C x 1-4-41-1-A	
	Anthesis-pollinated	Bud-pollinated	Anthesis-pollinated	Bud-pollinated
1	1	5	0	17
2	0	0	0	21
3	0	15	0	0
4	0	0	0	15
5	0	16	0	5
6	0	0	0	22
7	0	14	0	16
8	0	0	0	7
9	0	14	0	14
10	0	18	0	23
11	0	13	0	16
12	0	7	0	10
13	0	22	0	....
14	0	12	0	....
15	0	4	0	....
16	0	3	0	....
17	....	2	....	....
18	....	6	....	....
19	....	4	....	....
20	....	5	....	....
Total	1	160	0	161
Average	0.63	8.0	0	13.42

These results are explained by a genetic theory which was first worked out by East[4] in *Nicotiana*. This theory assumes the presence of factors in the pollen grain and in the style which prevent growth of the pollen tube when the factors are alike, but have no influence if the factors are different. Kakizaki[6] has studied the compatibility relations within the cabbage varieties Succession and Toyodawse and finds that a very similar mechanism was in operation. He also discovered that self-compatible plants occur, but do not breed true, only half of their progeny remaining self compatible. For a discussion of these theories, the reader is referred to the original papers.

BREEDING METHODS

Since experience has shown that in *Brassica oleracea* incompatibility factors are usually present which prevent the usual methods of purification of strains by inbreeding, a technique must be used which takes these factors into account. A method known as bud-pollination developed by the writer and used since 1926 has given uniformly good results, in so far as the incompatibilities are concerned. The process has grown out of a statement by Roemer[(11)] that optimum results in crossing were secured when the pollen was applied one or two days before the flower normally opens. Recently bud-pollinations have been recommended by Nilsson[(8)] for practical breeding work with radish. Noguti and Hamada[(9)] likewise have found in rice that early pollinations—applications of pollen while the flower was still enclosed in the sheath—gave a high percentage of fertilization.

Bud-Pollination.—The technique of bud-pollination has been described in a previous paper.[(10)] It consists of applying pollen to the stigmas of unopened flowers. This early application of pollen insures a normal set of seed. It probably allows the pollen time in which to germinate and send its tubes to the ovules before the inhibiting substance within the pistil has been elaborated.

As this method requires considerable personal attention to each plant, the technique and equipment will be described in detail in hope that they may prove useful.

The implement found to be most satisfactory for opening the bud is a pair of curved-tip forceps about four inches long. The tips should be very sharp, and parallel when closed. The bud is opened by inserting the tips of the closed forceps between two sepals and allowing the spring in the instrument to spread them, thus exposing the stigma. All the buds along the raceme over 4 mm in length should be opened.

The stigma is exposed by squeezing the opened bud between the fingers of the left hand. An anther which has just dehisced is taken from a protected flower with a pair of forceps, and the stigmas are touched with the pollen-covered surface of the anther. The mass of pollen can easily be seen with the naked eye.

The tips of the sepals need not be removed. The protection from drying which the sepals give, even though the flowers are split, will probably assist in the germination of the pollen. A tag is tied directly beneath the lowest treated bud; it gives the necessary data concerning

all the flowers opening above it. The writing should be protected from the weather, fungi, abrasion, and the action of wasps by a coat of white shellac.

After pollination, the raceme is covered with a one-pound manila paper bag (fig. 2), the mouth of which has been lined with cotton. This lining prevents passage of insects into and out of the bag—a consideration important in respect to thrips and aphis. Aphis multiply rapidly under the protection of the bag and by their sucking cause an atrophy of the younger buds. If they are present on the raceme

Fig. 2.—Branches bagged to isolate broccoli flowers. Salinas, 1931.

tip, a mature ladybug placed in the bag will destroy them. The cotton lining also serves as a cushion for the branches, and because of it the bag may be tied much more tightly with less chance of injuring the stem. The lining is about 1½ inches wide and is fastened to the paper with rubber cement. The cost of treating a thousand bags in this way is from $12 to $15. A bagged branch should be tied to other branches of the same plant rather than to a stake, because if the plant is blown by the wind the whipping effect will break a branch that is tied to a stationary object (fig. 2).

In going from one plant to the next, the forceps should be sterilized in alcohol containing a small quantity of formalin. A convenient field kit designed by the writer for pollination work is shown in figure 3.

After three to five days, according to the temperature, the plant should be visited again as additional buds will be ready for pollination. The plant may be visited several times, and from 12 to 20 flowers on each branch treated at each visit. As a rule the later visits require less time than the first.

As the pistils are receptive for four or five days after anthesis, the bag should be kept on the branch until the last flower has faded

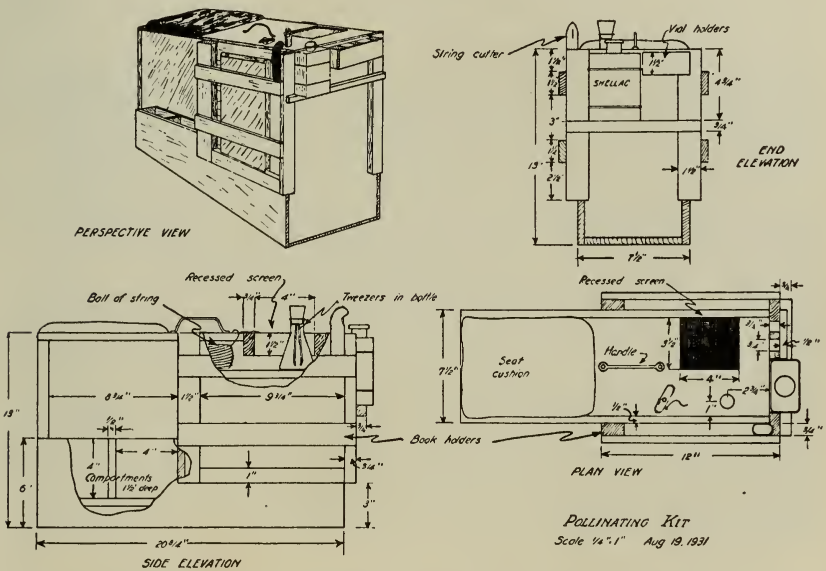

Fig. 3.—Kit for use in pollinating plants whose flowers are borne from two to four feet from the ground. The original box was made from a 7½ x 13 x 20-inch packing case; a seat cushion of burlap sacking adds greatly to one's comfort. The essential parts are: a flask for the sterilizing solution used for the forceps; string conveniently arranged near the knife blade; recessed box to hold tags, etc.; and holders for notebooks.

and the petals fallen. The stigma may, however, be pinched out cf each flower the second day after pollinating, the bag removed, and the seed allowed to mature. If the plant is kept in the bag, much light is prevented from reaching the siliques, and the seeds do not fill properly. Apparently a great deal of the food of the embryo is elaborated by the chlorophyll in the cells of the silique.

About a month after pollination, according to the temperature, the seeds are mature enough to germinate. Fifty per cent germination was secured at Davis 33 days after pollination when the seeds were planted directly in the soil.

Sparrows and linnets break open the pods and eat the seed. For this reason the pollinated branches should be rebagged for protection as soon as the embryo fills the seed. This procedure also save loss from shattering.

Hand-Pollination after Anthesis.—A method which was previously used but which did not allow for the condition of incompatibility was the application, by means of a camel's hair brush, of own pollen to the stigma after the flower opened. This method has been in common use, and most of the progress made in cabbage breeding has been accomplished by it. Very seldom, however, are more than one or two seeds formed in each silique, whereas normally the number is more than twelve. For rapid progress in breeding highly heterozygous plants, large numbers from which to select are necessary.

A further refinement of this method is the one used in Europe, as described by Becker,(2) where the racemes are protected by a glass flask supported upon a stick.

Caging.—In the plant breeding stations of the large seed companies, isolation of the entire plant under muslin cages has long been practiced (fig. 1). Pollination is by chance. The cages are usually knock-down, of wooden frame construction, covered with a medium or heavy-weight unbleached muslin. A modification, cheaper in construction and less expensive to store, is the use of short lengths of wire fencing the height of the plant, placed in a circle about it and covered with a sleeve of muslin which is gathered tightly at the top.

The disadvantages of caging are numerous. The result sought, production of seed, is not realized to any extent. As stated earlier, 100 seeds from each plant is a high yield; more often only 15 to 20 are secured. The cabbage flower is not adapted to self-pollination; the anthers bend away from the stigma; and, unless the flower is visited or disturbed, pollen will not fall upon the stigma. Even if pollen does reach the stigma, it may not be able to bring about seed formation. The protection and shading, furthermore, offer ideal conditions for certain insect and fungus pests. Aphis multiply very rapidly, and the cages must be opened every few days for dusting or spraying. Cauliflower or cauliflower broccoli is, furthermore, very susceptible to attack by *Bacillus carotovorous;* and, under the conditions of higher humidity and shading afforded by the cages, the plants soon succumb. Becker(2) describes a modification of this method where, instead of muslin, wire mosquito netting is used. This device would undoubtedly permit better aeration and easier insect control; but under California conditions it would not be efficient in securing total isolation, for

the smaller cuckoo bees (*Nomadideae*) could crawl through the mesh of the screen.

Fencing.—Of interest, but not of very great importance, is the method used by many gardeners in the isolation of their seed plot. The selected plants are massed, and a fence taller than the tallest branch is built around them (fig. 4). The crevices are carefully covered, since these gardeners believe that if the plants within the cage "see" the plants outside, crossing will result. While the explanation given is of course not literally true, the underlying fact is

Fig. 4.—Open-top cage for partially isolating groups of Brussels sprouts plants. Half Moon Bay, 1931.

sound, being based on the flight characteristics of the honeybee. While en route to or from the hive the bee travels in a "bee line," about 10 to 15 feet above the ground; while gathering honey or pollen it stays very close to the level of the plants on which it is working and visits only plants having the same type of flower. Thus a fence placed about a group of plants so that the bees cannot see other plants while working these plants, or these plants while working others, will decrease the amount of crossing to a large extent. The special types which have been developed by growers who save their seed by this method speaks well for its efficiency. It could hardly be applied to single plant isolations.

BREEDING PROGRAMS

The fact that a system of compatibilities exists, in the species *Brassica oleracea,* must be considered in the development of a program of breeding. In general, there are two methods of improvement of plants: (1) mass production of seed, accompanied by careful roguing; and (2) self-pollination or isolation of promising or ideal individuals, further selection within their progeny, and finally increase of the purified line. This second method, known as the "progeny test," was first used by Vilmorin in 1856 (Hayes and Garber).[5] It is the method usually employed today in the improvement of plants by selection.

This pedigree method, necessitating constant inbreeding, will in the course of a few generations—usually considered to be seven—result in practically pure lines, homozygous for nearly all characters. Thus uniformity and quality can be secured in a relatively short time. A serious drawback to the method, however, is the matter of vigor. Loss in vigor has been noted in many normally cross-pollinated plants after a few generations of inbreeding. The loss is not uniform, however, for in certain lines the decrease is less than in others, and in maize for instance (Collins)[3] some inbred lines have been found to be fully as vigorous as the original variety.

Cabbage, cauliflower, and cauliflower broccoli, being highly heterozygous, lose vigor to a considerable extent with inbreeding. Uniformity is secured, but the plants mature later and are smaller than those of the same variety similarly treated but not inbred. As a market commodity, however, smaller, finer-textured products are desirable, so that loss in vigor in itself is not always a serious fault.

The relation of compatibilities to seed production is important. A line made pure for vegetative characters will, unless special precautions are taken, be pure for the factors regulating pollen tube growth, so that the plants would be sterile to their own pollen or to pollen from other plants of the same line. This means that a line could not be propagated by seed unless the inhibitory substance could be avoided in some such way as bud-pollination, which is of course expensive and impossible to use except in breeding operations. Some plan must be followed which will circumvent the incompatibility situation. Two methods are possible: first, a program of alternate selfings and massings, designed to keep the line heterozygous for the inhibitory factors; and second, a program of intensive inbreeding to purify the lines, followed by the mating of pure lines in compatible combinations for the commercial production of crossed seed.

Alternation.—The method of alternation of selfings and massings is relatively simple; but several years longer will be required for purification of the lines, and the final result will be different from that obtained by the method of commercially producing crossed seed. It is summarized in figure 5.

The first step consists of selfing by bud-pollination of the plants originally selected, and then growing a large population of the progeny of each. As many plants as possible should be grown, since a great

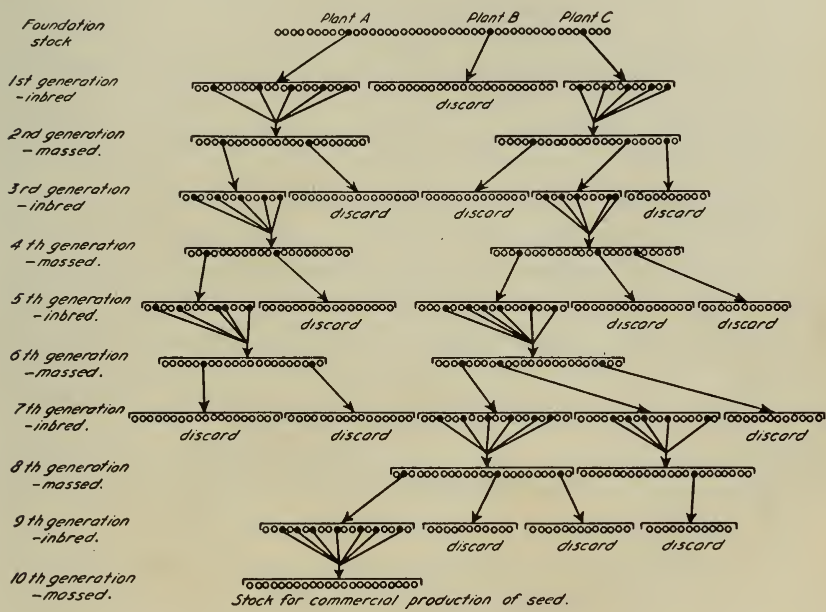

Fig. 5.—Chart showing the suggested plan for improving cabbage varieties by the alternation of inbreeding and massing.

many of the commercially important characters are quantitative in inheritance. Selection should be critical, and perhaps a dozen plants of the same type from each line should be finally chosen for propagation. The number may be smaller, but not less than four or five should be saved. They are then open-pollinated among themselves and massed; the seed is lumped together and planted. Critical selections are again made from this population. The selected plants are bud-pollinated, each plant thus giving rise to a new line. Again, out of each line, several plants of the same type are selected and massed, the mass from each line being, of course, kept isolated. Selection is made the next year, and these related plants are selfed, and so on until the desired degree of perfection has been reached. The result

is a strain that can be propagated by natural means. In all probability, however, the vigor of the new strain will be somewhat less than that of commercial lots.

In figure 5 an example of such a system of breeding is given. The first year selections, such as plants A, B, and C, are made from the foundation stock. Each of these plants is selfed by bud-pollination, and the following year a large number of the progeny of each plant grown. In the example, the progeny of plant B was inferior to that of A and C, so it was discarded. Five of the best plants in the progeny of A are selected and planted in a location isolated from other *Brassica oleracea* plants. Similarly five plants were taken from the progeny of C, and planted together but in a different place from those from plant A. These are open-pollinated, and the seed produced by each plot kept separate. It is not necessary to keep the seed from each plant separate, however. The next year a large number of each lot is grown. These should be gone over carefully, and only the very best saved. These plants are selfed by bud-pollination, and their progeny grown the following year. At this time it may be desirable to discard certain of the progenies, as shown in the third generation on the diagram. In a similar way the program is carried along in succeeding years. It may develop, as in the seventh generation of this example, that one line is superior to another; the inferior line should be dropped. As soon as the desired degree of improvement has been reached the line can be increased for commercial use.

By this program the plants have been purified for the visible characters and kept heterozygous for the invisible compatibility factors. The open-pollination among the members of a family inbred for one generation each time gives a chance for the unlike pollen tubes to function. About half the plants so isolated for massing may be expected, however, to set seed very poorly. These would be the heterozygous plants for the incompatibility factors.

The yield of seed per plant, however, when produced on a commercial scale after following the above program, can be expected, on theoretical grounds, to be much lower than the seed yield from plants of unselected varieties. This would be the result of the action of the incompatibility factors. The only kind of plant that is formed by the massing of an inbred line is one heterozygous for the incompatibility factors; groups of plants heterozygous for the same factors are as self and cross incompatible as plants homozygous for these factors. Kakizaki,[6] however, has shown that there are minor factors present in cabbage which permit the formation of some seed, so that

by their action the line can be increased. The breeder who follows this program must be prepared to accept radically lower yields of seed.

Crossing.—The method of producing crossed seed requires more care. It will give the grower a monopoly of his particular strain, so that the latter cannot be reproduced by others from his commercial seed without many years of careful breeding work. This plan is summarized in figure 6.

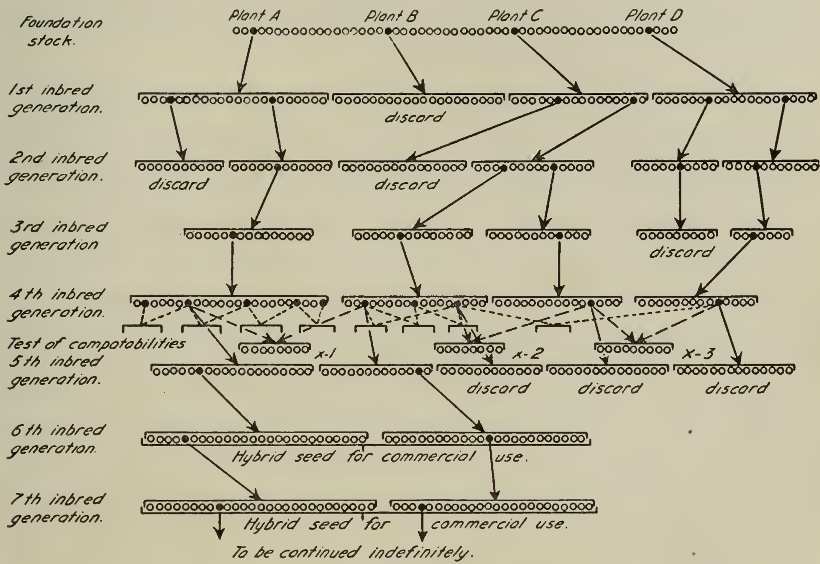

Fig. 6.—Chart showing the suggested plan for producing hybrid cabbage seed commercially.

The first step is to purify the lines by bud-pollination and selection; three or four generations should suffice for practical purposes. Then the lines should be tested for self and cross compatibility. One method is to cross-pollinate by hand after the protected flower opens. Fifteen to twenty flowers at least should be tested in this way, the tests being made reciprocally. If negative results are secured, the plants are identical in compatibility factors; and if the results are positive in both directions, the plants have different factors. If the cross is successful in one direction and unsuccessful in the other, the pollen parent of the unsuccessful cross is homozygous or pure while the pollen parent of the successful cross is heterozygous or impure for these compatibility factors. The plants likewise should be tested for self compatibility, since lines breeding true to self incompatibility must be used.

The alternative method of testing for compatibilities is to plant several individuals of two lines together in isolated locations, to test their ability to set seed. This plan is expensive and requires much attention to the plants.

The seeds from compatible crosses should be planted to see whether they produce the type of plants desired. If the cross has been between unrelated or distantly related plants, an increase in size of plant should usually result. If the cross is between closely related plants—brother-and-sister matings—little difference will probably be found between the hybrid and the parents.

The desirable type, once secured, can be produced in quantity by simply planting the two lines together. The lines, being homozygous, can be perpetuated by bud-pollinating a few branches on several plants of each line; and hybrid seed can thus be produced in commercial quantities each year. Crosses between pure lines are uniform.

In figure 6 the procedure to be followed in the production of hybrid or crossed seed is diagrammed. Selections are made from foundation stock and selfed as described before. Further selections are made from the progeny, and selfed again. Selection in this case should be very critical. Progenies from several original plants should be carried on. Entire lines should be discarded if they fail to show the desired quality. By the fourth generation the lines should be approaching uniformity. At this time the compatibilities should be tested. These tests are shown in the diagram as dotted lines. Those which failed do not have circles beneath their brackets. In this example, the cross between a plant of line A and one from line C proved to be superior in vigor and quality to those crosses involving C and D. These are presented in the diagram as X–1, X–2, and X–3. It would be expected that X–2 would be inferior, since it is between two plants separated by three generations although descended from the same original plant.

Since X–1, involving A and C, was found to be superior, selfed progenies of plants of these lines are planted in alternate rows in the seed field. The open-pollinated seed is hybrid in origin. The lines can be perpetuated by bud-pollination and hybrid seed produced in commercial quantities each year.

Owing to the usual loss in vigor resulting from inbreeding *Brassica oleracea* the success of this method will depend upon making selections which are vigorous in each generation. Since it is practically inevitable that vigor will be lost, extra care must be given the seedlings in establishing them in the field.

However, a monopoly can be secured by a grower who combines two types, distinctly different. The hybrid, usually intermediate, will be uniform and vigorous; but plants selected from this lot for seed will produce a segregating population.

SUMMARY

Flower buds open about four weeks after they are differentiated. The floral organs appear in this order: sepals, petals, stamens, and pistil.

Anthesis usually begins late in the afternoon and is completed early the next morning. Pollination is by insect visitation, chiefly by bees, both honey and solitary. Nectar is secreted by the two nectaries between the outer stamens and the pistil.

Pollen retains its viability from six or seven days at 50° F to two days at 95° F and 39° F. Optimum germination was secured at 68° F in 20 per cent sucrose solutions. Germination was secured at temperatures ranging from 46° F to 80° F. Abnormal germination was secured at 86° F or above, and no germination at 104° or 39° F.

Own pollen is less efficient than cross pollen in causing seed formation. At Davis 6 per cent selfing was secured in double pollinations, probably because of the operation of a system of incompatibility factors similar in many ways to that described in *Nicotiana*. Kakizaki has obtained similar results for cabbage. Early pollinations of incompatible plants give a good set of seeds.

A method, with description of equipment and of technique, is given which circumvents the action of the inhibitory substance. This is generally known as bud-pollination. Other methods—caging, hand-pollination, isolation—are described.

Two programs of breeding *Brassica oleracea* forms are proposed which take into account the compatibility situations present.

The system of alternation of selfing and massing requires a longer time to reach a given degree of uniformity than a system of straight inbreeding. By means of massing, however, the strain is kept heterozygous for the compatibility factors. Loss of vigor will probably accompany this system.

The system of producing crossed seed commercially requires the development of pure lines of self-incompatible plants which are inter-compatible. Planting these lines together will permit the formation of crossed seed, producing plants having hybrid vigor and the uniformity of the hybrid. The pure lines can be perpetuated by bud-pollination.

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